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Critical Literature Review
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Plants on the edge: How will Antarctic mosses respond to global environmental change?

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Abstract

The extreme conditions of the Antarctic continent represent a significant barrier to life. Vegetation of terrestrial Antarctica is restricted to regions free of ice, which make up only 0.3 percent of the continent. Antarctic plants live at the physiological limits of survival. Land plants are mostly confined to the cryptogams: mosses dominate the ice-free land and can form complex communities in areas that receive adequate summer meltwater. Intrinsically, Antarctic mosses represent unique diminutive communities at the limits of survival, ecologically they provide habitat for invertebrates, and globally they can be seen as sentinels for global environmental change. There is evidence for rapid environmental change already occurring on the Antarctic continent: the Peninsula is one of the fastest warming regions on the planet, East Antarctica is undergoing warming and drying, and the entire continent is subject to high UV-B levels as a result of ozone depletion. Already at the limits of survival, Antarctic mosses are likely to be particularly sensitive environmental change. Indirect effects of climate change such as water relations will probably have a greater impact than rising temperatures alone. Mosses may benefit from the short term reduction in stress that follows warmer temperatures. However the long term effect is more complex, particularly combined with competition from invasive species interactions. Community level shifts in moss distribution and diversity are likely, as well as possible local extinctions. Understanding the response of moss communities to environmental change requires a combination of long term field studies, incorporation of new technologies and continued monitoring programs, including conservation plans in a proactive response.

Plants on the edge: How will Antarctic mosses respond to global environmental change?

Extreme environments: a barrier to survival

Terrestrial Antarctica is an extreme environment where organisms are subject to harsh conditions of punishingly low temperatures, high aridity, severe winds, strong seasonality, divergent light changes and short growing seasons. The continent is isolated by the vast expanse of the cold Southern Ocean, and most of Antarctica is locked in ice. These conditions represent a significant barrier to survival. Antarctic vegetation is constrained to the regions free of ice, which makes up less than 0.3 percent of the entire continent (Convey et al. 2008). Terrestrial life is bound to the land, and exposed to its severe conditions.

Antarctic plants: why moss?

Antarctic plants live ‘on the edge’, at the physiological limits of survival (Robinson et al. 2003). Only two vascular plants occur on the continent, the grass *Deschampsia antarctica* and cushion plant *Colobanthus quitensis*, and even these are restricted to the relatively mild conditions of the coastal Antarctic Peninsula (Alberdi et al. 2002). The harsh Antarctic conditions constrain plants to the diminutive. Antarctica is the land of the cryptogams: bryophytes, lichen and algae. Mosses are the dominant plant species of continental Antarctica, and they may be considered the ‘rainforests of the poles’ (figure 1). Mosses are bryophytes: spore-producing non-vascular plants with simple leaves (Ochyra et al. 2008). Populations are sparse, growth is slow, and dispersal is difficult (Skotnicki et al. 2004).

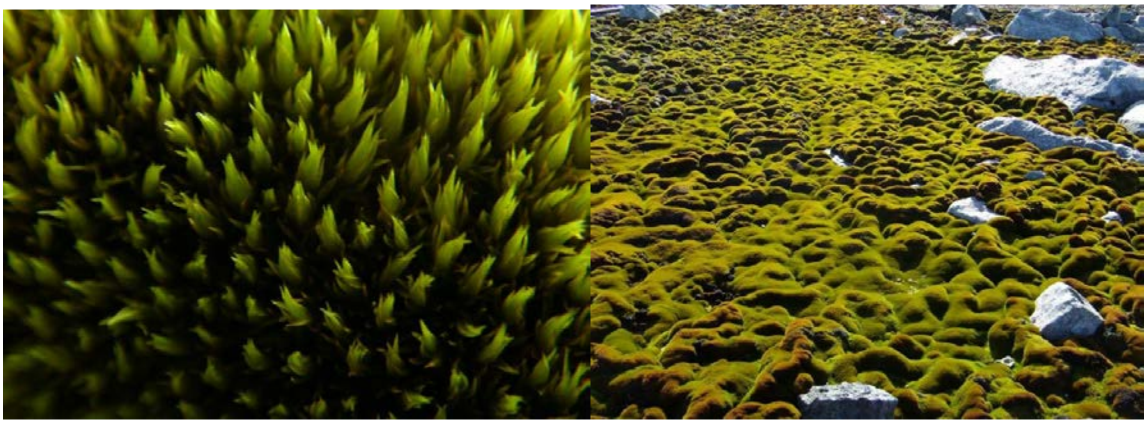

Figure 1: Mosses (left) are the dominant plant life in Antarctica, and may be considered miniscule forests. They can form extensive moss beds, such as these pictured (right), from the Windmill Islands near Australia’s Casey Station in East Antarctica.
Left image: Roger Kirkwood; Right image: Sharon Robinson

Scope

Antarctic mosses exist at the limits of their survival, so even small environmental variation can have a major impact on these communities (Robinson et al. 2003; Convey and Smith 2006). Environmental change, such as human-mediated climate change and ozone depletion are expected to heavily impact the high latitudes (Wasley et al. 2012; Newsham and Robinson 2009). The Antarctic Peninsula is one of the most rapidly warming regions on the planet (Royles et al. 2013), and continental Antarctica is similarly vulnerable to environmental change (Wasley et al. 2006b). Therefore Antarctic mosses could be significantly impacted by environmental change. Since they represent a unique ecosystem, and are sensitive to change, it is important to understand their responses, in the context of their distribution, ecology adaptations and importance.

Biogeography

The Antarctic continent is divided in to two sections based on climate and biota (figure 2): maritime and continental Antarctica. Maritime Antarctica is generally defined as the western band of the Antarctic Peninsula, down to 72°S, and up to the South Shetland Islands, South Orkney Islands, Bouvetøya, South Sandwich Islands (Peat et al. 2007). The maritime is influenced by the Southern Ocean, with average temperatures in summer reaching 0-2°C (Convey and Smith 2006). The continental Antarctic comprises the eastern side of the Peninsula (below 63°S) and all East Antarctica, including the Balleny Islands (Peat et al. 2007). Temperatures are low, frequently below 0°C even in the summer months (Convey and Smith 2006).

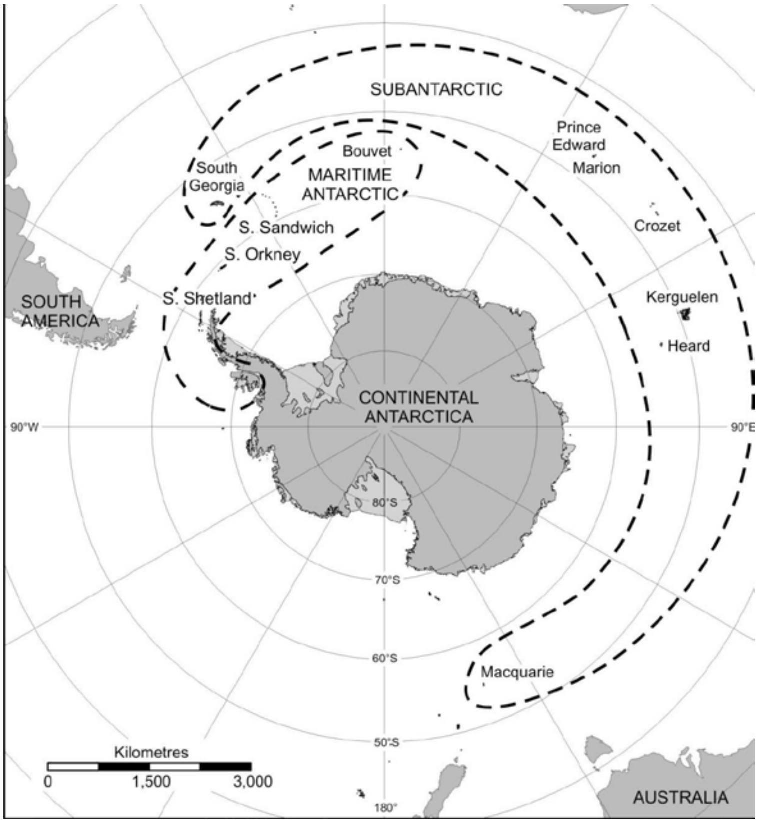

Figure 2: Antarctica is split into three major biogeographic regions: the Sub-Antarctic, the Maritime and the Continental regions. This review considers 'Antarctic mosses' as those from the maritime and continental regions.
Image: Peter Convey

Before we can understand the future of Antarctic mosses, they must be placed in an evolutionary, ecological and environmental context. It is thought that mosses are recent colonists to Antarctica, existing since the last glacial maximum approximately 20,000 years ago (Convey et al. 2008). Today, moss diversity generally decreases with higher latitude (towards the South Pole), across the sub-Antarctic, maritime and Antarctic continent, but not within the continent (Cannone et al. 2013; see table 1). The highest moss diversity on the continent is found on the Peninsula (Peat et al. 2007). Moss diversity in the continent appears to be driven by local scale microenvironments rather than these latitudinal gradient patterns (Cannone et al. 2013). They are restricted to areas that receive liquid water during the summer melt (Wasley et al. 2006b), so distribution is largely bound to physiology. In the maritime, mosses can occupy 'fellfield' habitats, extreme environments of low temperatures and water stress (Pannewitz et al. 2005). Other communities may exist in regions of regular meltwater, exposing them to water inundation (Pannewitz et al. 2005). Mosses can also be found clustered around active volcanoes in geothermal habitats, where they form distinct communities (Convey and Lewis Smith 2006; Skotnicki et al. 2002).

Table 1: Approximate numbers of moss species found in each of the three major regions of the Antarctic (Adapted from Cannone et al. 2013 and Peat et al. 2007)

Antarctic Region	Number of moss species
Sub-Antarctic	250
Maritime	110
Continental	25

Adaptations

Bryophyte growth is controlled by the severe conditions and high seasonality of the Antarctic. Mosses are subject to the significant stresses of the harsh environment: temperature extremes, water stress (desiccation and submergence), limited nutrients, variable light radiation, high winds, and continuous sun in summer and prolonged darkness in winter (Convey et al. 2008). Their simple structure means they take up water and nutrients passively (Robinson et al. 2000). Like other cryptogams, they can tolerate and recover from excessive drying out (desiccation), and extreme cold by becoming dormant (physiologically inactive) during times of low water availability, an adaptation called poikilohydry (Robinson et al. 2003; Pannewitz et al. 2005). Mosses can also tolerate submergence from spring melt water (Melick and Seppelt 1997). They stop photosynthesising under stressful conditions such as desiccation or high levels of solar radiation, meaning that growth is slow, only a few millimetres in a year, and a single moss shoot can be hundreds of years old (Robinson et al. 2003). Mosses lie dormant during the cold, dark winters, becoming active again during the spring snow melt (Robinson et al. 2003).

Importance

In a continent bound and shaped by ice, bryophytes of the Antarctic represent diminutive communities of great importance. The harsh, isolating conditions constrain vegetation to the miniscule, and intrinsically, mosses characterise unique, isolated communities at the limits of survival. Ecologically, they represent one of the simplest ecosystems on the planet, with few biological interactions (Robinson et al. 2003). The relative absence of herbivores (grazers) and disease in Antarctic environments means that moss communities are mostly fashioned by environmental constraints, rather than biological interactions (Wasley et al. 2006b). Antarctic moss communities can be used as a baseline for measuring the study of evolution and adaptation in extreme environments (Convey and Smith 2006). Existence at the limits of survival means it is likely that Antarctic mosses may be more sensitive and responsive to change, so globally, they can act as sentinels for environmental change (Robinson et al. 2003).

Environmental change: climate change and ozone depletion

Much of the work on Antarctic mosses and their response to environmental change has been performed in the Windmill Islands, in East Antarctica. It has some of the most well developed moss beds on the continent, with three co-occurring moss species, and has been the site of long term monitoring (Wasley et al. 2012; Robinson et al. 2003; Robinson et al. 2000). These studies are important, because they show community level responses and species dynamics. The Windmill Islands are already thought to be experiencing environmental change in the form of a drying climate (Melick and Seppelt 1997). The Antarctic Peninsula is also undergoing rapid climate change, where temperatures have risen by 0.5°C per decade since the 1950s (Royles et al. 2013; Turner et al. 2009). The entire continent receives heightened levels of ultraviolet-B radiation as a result of ozone depletion, particularly pronounced in spring (Clarke et al. 2009). Quantifying long term change in these regions is essential to determine whether Antarctic mosses can cope with this rapid environmental change.

Climate change

Water availability: a case study from East Antarctica

Availability of free water is one of the most limiting factors for life in polar deserts (Kennedy 1993). It has been suggested that the indirect effects of climate change, particularly water availability, will have a greater influence on moss growth than temperature increases alone (Wasley et al. 2006a). Climate change may cause a warmer, wetter, or warmer, drier climate in the Antarctic over the long term, so how a moss species or community responds to water stress is critical in determining their future under climate change (Wasley et al. 2006b). The ability to tolerate drying may improve a plant species long term chances of survival (Wasley et al. 2006b). In the short term, more water may be available to mosses, since increasing temperatures will promote greater summer melt (Wasley et al. 2012). It is possible that wetter conditions could cause moss beds to become submerged, so tolerance to water inundation is also important.

The three species comprising the Antarctic moss community of the East Antarctic Windmill Islands *Schistidium antarctici* (formerly *Grimmia antarctici,* endemic to Antarctica), *Ceratodon purpureus* (cosmopolitan) and *Bryum pseudotriquetrum* (cosmopolitan), displayed varying ability to tolerate desiccation and submergence conditions (Wasley et al. 2006b; Robinson et al. 2000; Wasley et al. 2012). These species all have distributions bound to water availability. Previous studies in this region have suggested that the climate of the Windmill Islands may have been wetter in the past, and may be already subject to long term drying (Melick and Seppelt 1997). Continued, long term drying of the climate as is likely to cause moss habitat to contract, since mosses are restricted to areas of adequate free water (Wasley et al. 2012). By using quantitative fine scale methods, the recent study by Wasley et al. (2012) provides a model for baseline monitoring of the future community change: prediction of future change requires knowledge of current distributions and environmental variables driving change.

Notably, the water availability studies indicate that *B. pseudotriquetrum* has a flexible tolerance to drying and high desiccation avoidance due to its dense turf (tightly packed gametophyte shoots) while dried out, and the high sugar content (stachyose carbohydrate) within its cells. This species also showed a similar, highly flexible response to submergence, suggesting that *B. pseudotriquetrum* may not be as badly affected under a changing climate, since it can survive in both dry and wet habitats. It may expand into areas that are currently too wet (Wasley et al. 2012). *C. purpureus* had the highest desiccation tolerance, due to its tightly packed turf and high lipid content. However it had the lowest submergence tolerance, explaining its current restriction to drier sites. The endemic moss species, *S. antarctici* displayed the lowest desiccation tolerance, likely due to its loose turf, yet highest tolerance for submergence, reflecting its restriction to the wettest habitats. The studies further emphasise that current moss species distributions are bound to physiology, and that it will be physiology that will likely determine survival under a changing climate.

Ozone depletion and recovery: light radiation (UV levels)
Ozone depletion is the thinning of the ozone layer which occurs above Antarctica in the austral spring of each year (figure 3). This results in a high level of ultraviolet-B radiation. Ozone depletion in spring can expose mosses to high levels of UV-B radiation while they are desiccated (Turnbull et al. 2009). Exposure to high levels of UV-B can cause damage to DNA (Turnbull and Robinson 2009). Bryophytes were originally thought to be vulnerable to high levels of UV-B radiation, but recent studies have shown that some species of Antarctic bryophytes have a high tolerance to UV-B (Clarke and Robinson 2008; Dunn and Robinson 2006; Turnbull and Robinson 2009; Turnbull et al. 2009). For example, the cosmopolitan species *C. purpureus* and *B. pseudotriquetrum* are able to protect themselves from UV-B radiation while desiccated, suggesting that these species will be more able to tolerate elevated levels of UV-B exposure that is continuing to occur with ozone depletion (Turnbull et al. 2009).

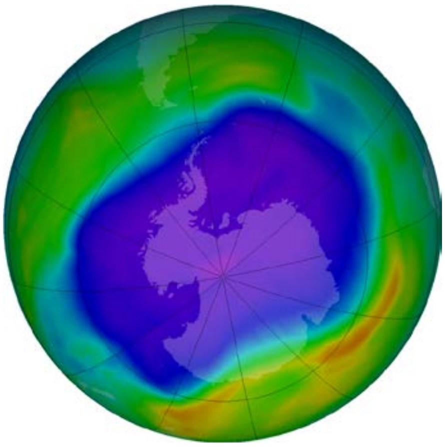

Figure 3: Ozone depletion (thinning in ozone layer) over Antarctica on 24 September 2013 (greatest recorded extent, in spring). Depletion of the ozone layer causes increased UV-B radiation, which will likely affect Antarctic mosses.
Image: NASA

Full ozone recovery is not expected until 2060 (Turnbull and Robinson 2009), so it is important to understand how ozone depletion will impact Antarctic mosses. The endemic Antarctic moss species, *S. antarctici* is unable to protect itself from high levels of UVB radiation while desiccated, which makes this species more vulnerable to ozone depletion (Dunn and Robinson 2006). Species growing in exposed areas can synthesise UV protective pigments (Newsham and Robinson 2009). UV-B could also effect pigmentation of moss as shown in studies with a species from the Antarctic Peninsula, *Andreaea regularis* (Newsham 2003). The effect of increasing UV-B radiation on Antarctic mosses is therefore complex, and likely to be subtle, with varying effects between species and across communities.

Long term species dynamics and diversity

Under a warmer, wetter future climate, healthy bryophytes will increase in abundance and distribution, and currently desiccated bryophytes could regenerate, with high species richness likely (Wasley et al. 2006b). Species which do not tolerate wetter conditions, such as *C. purpureus* may decline in regions that become too wet, and colonise habitats currently too dry for moss survival and growth (Wasley et al. 2012). At a community scale, moss communities may expand into areas too dry for moss survival at present. If the Antarctic climate becomes warmer and drier, healthy mosses will likely contract to smaller ranges (Robinson et al. 2000). Mosses well adapted to dry conditions are predicted to survive these conditions, and may shift distributions to colonise areas currently too wet (Robinson et al. 2003).

The current evidence shows that the endemic species *S. antarctici* is particularly vulnerable under a drier climate because of its low tolerance to desiccation and sensitivity to UV-B radiation, making it a target for potential future monitoring and conservation efforts. *S. antarctici* therefore has a higher risk of extinction in a changing climate (Wasley et al. 2012). As this species is endemic to the Antarctic continent and occurs nowhere else on Earth, loss of this species will be a loss for Antarctic and global biodiversity. Conversely, species that have greater plasticity and show a flexible response to water stress, such as *B. pseudotriquetrum* may be least affected by shifting water relations under a changing climate, and will likely continue to survive (Robinson et al. 2003). Under either climate change scenario, regions of transition between high and low water availability may provide important refuges for moss diversity (Wasley et al. 2012).

A more complex picture: interacting effects

Predicting the response of Antarctic mosses under environmental change is further complicated by the interactions of other variables, across a variety of different temporal and spatial scales, such as genetics, nutrients, and competition with invasive species. For instance, it is thought that Antarctic bryophytes may have relatively low levels of genetic variation, making them particularly vulnerable to environmental change (Clarke and Robinson 2008). However, estimations of genetic variation have suffered from sample contamination and lack of adequate replication (Clarke et al. 2009), meaning the true nature of genetic variation in Antarctic mosses has been difficult to assess. Climate change manipulations involving the interactions of nutrients and water, suggest that moss communities may react favourably to a warmer, wetter climate, only if nutrient availability increases along with water (Wasley et al. 2006a). Equally, any possible short term beneficial effects of reduced environmental stressors (for example greater water availability, more ice-free land), may be confounded by increased competition with invasive species (Chown et al. 2012; Chwedorzewska 2009). Evidently, predicting the long term future of Antarctic mosses under environmental change is complex and requires continued research into both singular and interactive effects.

Future directions

Long term, manipulative field studies, and monitoring are vital if any meaningful information is to be gathered on how bryophyte biota respond to environmental change (Robinson et al. 2003). Long term studies bring significant challenges in a harsh environment, observing a unique miniscule ecosystem, where change is slow. Repeated field studies have the potential to be damaging, with possible cumulative impacts. Long term vegetation studies in Antarctica are therefore a question of scale and of impact. New ways of studying and monitoring ecosystems, through technological advancements, will greatly benefit these developments. For instance, unmanned aerial vehicles (UAVs) have been shown to be effective at mapping small scale, high detail observations of moss beds by obtaining digital surface models and aerial photography (Lucieer et al. 2013; Lucieer et al. 2011). The future of long term vegetation field programs in the Antarctic should evolve with advancing technology, providing small scale, non-destructive, ultra-high resolution measurements, monitoring and prediction.

Community level, long term, field studies (both observational and manipulative) should be the future focus of Antarctic vegetation studies (Wasley et al. 2012), in concert with a number of other methods to provide a more complete picture of the response of Antarctic mosses to environmental change. Incorporating refined genetic studies can tell us the genetic diversity of particular moss species, and their capability for adaptation under environmental variation (Clarke et al. 2009). Superior long term modelling of the future of Antarctic moss communities under climate change scenarios will aid in prediction (Royles et al. 2013). Laboratory experiments provide an important compliment to field studies (Convey and Smith 2006). Complex interactions must be incorporated, particularly with increasing risk of invasive species (Chown et al. 2012), and unclear interactions of variables like nutrients and water availability (Wasley et al. 2006a) or UV-B damage and rising temperatures (Newsham and Robinson 2009). Long term monitoring programs, particularly with standardised methods, are vital to determine community and ecosystem level change in Antarctic moss communities (Cannone 2006). Monitoring and manipulative field experiments in Antarctica are particularly important to determine if conservation or management actions need to be taken (Wasley et al. 2012).

Conclusions

Antarctic mosses could benefit in the short term from environmental change, due to more ice-free areas of ground for colonisation and free water from increased summer melting. However, the long term future of Antarctic mosses is likely to be significantly altered under environmental change: with decreased diversity across a number of scales, possible local and continental species extinctions, shifts in distribution and changes in abundance. The ability of mosses to tolerate a warmer, drier or wetter climate varies, and their abilities to adapt to change are unclear, with some species more greatly affected than others. Complex interactions with other variables such as invasive species and nutrient relations makes the long term future of Antarctic mosses uncertain. Long term manipulative field studies, such as those established in the Windmill Islands of the East Antarctic are vital to gain a definitive understanding of the response of mosses to environmental change, and to provide a baseline for change monitoring.

Ideally, long term studies could be systematically developed across the Antarctic continent, in international collaborative scientific efforts, to gain an understanding of continental scale change. Long term programs will only be effective if coupled with other methods such as genetics, modelling, laboratory studies, non-destructive technologies and inclusion of complex interactions like invasive species competition. Precautionary conservation programs should be considered for species such as *S. antarctici* which may face extinction under environmental change. Since climate change is projected to affect the polar latitudes first and hardest, significant moss community shifts could be a precursor to similar changes in other taxa. Significant environmental changes are already apparent, with temperature increases in the maritime and high UV-B radiation associated with ozone depletion. In the harsh polar desert of the Antarctic continent, diminutive moss communities largely represent the terrestrial vegetation. Antarctic mosses are unique, yet vulnerable communities that provide a baseline for detecting global change. A commitment to understanding the response of Antarctic mosses is vital for protection of these exceptional communities, and for knowledge and predictions of global environmental change.

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